THE ANATOMY OF THE CONIFERALES.

(*Continued from page 359*).

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Resinous Tracheids and Resin Cells.

The investigations of Eichler (11, p. 35) show that in Ginkgo the wood is characterized by the presence of wood parenchyma elements which take the form of short idioblasts of a lenticular form in longitudinal section, and are distinguished by the storage of crystals of calcium oxalate. These structures are peculiar to this genus in which they form a specific character of definite value, but a more detailed account of them at this time is not called for.

In a large proportion of the Coniferales the wood is characterized by the presence of more or less numerous wood-parenchyma cells. These are always distinguished by their cylindrical form and transverse terminations. They are invariably associated with the production of resin, either as entering into the composition of resin passages, or as isolated cells. It is this latter group with which we are most particularly concerned at the present moment and as, with very few exceptions, they are uniformly characterized by the presence of resin which gives them a distinctive appearance, I prefer to describe them as "resin cells" rather than by the more commonly employed designation of "wood-parenchyma," which conveys no suggestion of their special function and most prominent feature.

Before proceeding to consider these structures more in detail, it will be necessary to digress for a short time and discuss certain other elements which have been erroneously regarded as wood-parenchyma. It has been stated by Eichler (11, p. 35) that wood-parenchyma elements occur in Araucaria and Agathis, but this is evidently due to a wrong interpretation of certain features presented by species of those two genera, which, according to

our investigations, are wholly devoid of such structures, in the sense defined above.

In *Araucaria excelsa* a transverse section shows more or less numerous elements containing resin. These are not to be distinguished in their general structure from the surrounding tracheids, and they are to be recognized solely by their contents, which are usually somewhat prominent. Their distribution is characteristic. They occur in small, scattered groups, or more commonly in rows one or two elements wide, parallel with the medullary rays and in immediate contact with them on each side. When the plane of section passes near the position of the supposed terminal walls the latter may be seen to be cut through in various ways, but they never exhibit any structural features, and they are therefore in no way comparable with the terminal walls of the wood-parenchyma cells. In a radial section they are seen to be long and fusiform, exactly resembling the wood tracheids, except for a reddish brown transverse plate which occurs either close to or exactly opposite a medullary ray, a position which is more clearly shown in a tangential section (Fig. 35). The dark plates closely resemble Sanio's bands, for which they might very readily be mistaken upon casual observation, or they might likewise be mistaken for terminal and unpitted walls. In *Agathis australis* these features are represented in their typical form. The transverse section shows such elements to be numerous and disposed in radial rows on each side of the medullary ray (Fig. 32). In a radial section they present the same fibrous and fusiform character as in Araucaria, but in addition the wall usually experiences a marked increase in secondary growth within a region exactly opposite the ray (Fig.

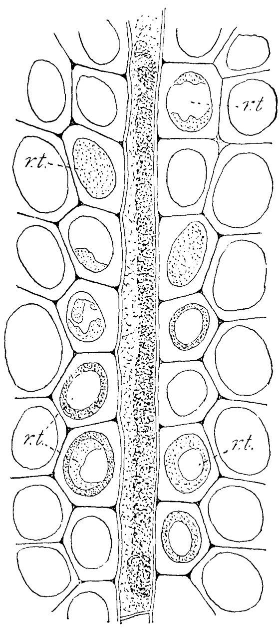

FIG. 32.—*Agathis australis.* Transverse section showing the disposition of the resinous tracheids on opposite sides of the medullary ray at *r. t.* × 300.

33). This feature is also prominent in a transverse section (Fig. 32). Such local increase in thickness always arises in adjacent cells in such a way that the more strongly thickened regions are exactly opposite, and they serve to constrict the cell cavity gradually from above and below in such a way as to leave a channel about half the usual width of the cell cavity, which gradually widens upward and downward (Fig. 33). It is at the position of maximum constriction that we find a transverse plate of variable thickness, but always of a reddish brown color. These plates are always thinnest in their central region, and they may be of uniform thickness for the greater part of their extent. At the region of contact with the tracheid wall they become thicker and thereby attain a vertical distribution to an extent four or five times greater than the general thickness. At such position also there is somewhat clear differentiation between the plate and the wall in point of color. Such plates show absolutely nothing of the nature of pits, and they are in no sense comparable with the terminal walls of the wood-parenchyma cells, except in form and position (Fig. 33).

The peculiar position of these plates, their resinous color and their simulation of both Sanio's bands and terminal walls, excited a suspicion as to their true nature and led to the belief that they might not be structural features at all. They were therefore subjected to a series of careful tests to determine (1) if they were structural, (2) if they were resinous, and (3) if the latter, to what extent. It was recalled in this connection that, although devoid of any special secretory reservoirs in the wood, Agathis is nevertheless well known for its production of the resin called gum dammar. It was suspected that the plates might be local deposits of resin, and they were therefore brought into direct comparison with gum dammar,

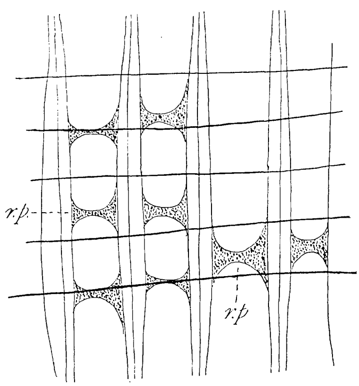

FIG. 33.—*Agathis australis*. Radial section showing the local thickening of the tracheid wall, and the occurrence of resin plates (*r. p*) opposite a medullary ray. × 225.

the characteristics of which are well known and described by Wittstein (D. 53, p. 63). Tests were applied to thin radial and tangential sections, employing for this purpose (1) various essential and fixed oils, (2) ether, (3) alcohol, (4) ammonia, (5) potassium hydrate in one and one half percentage solution. The plates were found to be very refractory with respect to both the fixed and essential oils, as well as towards ether, alcohol, ammonia and xylol, and in all of these cases no change was to be observed, even after an action extending over several weeks. A partial exception applies to alcohol and ether. In the latter case there did appear to be a certain diminution in volume, apparently through solution, when the reagent was first applied, but after that there was no further alteration. The application of alcohol, both in the hot and in the cold, showed that while the resin contained in the medullary rays was all dissolved, the plates were only partially affected. The reaction of the reagent was chiefly manifested in the development of strong curvature, often accompanied by fracture. This was evidently due to an increase in volume, and a tendency toward solution, and it gave the first definite evidence that the plates could not be of a cellulose character. Beyond this no further change was brought about, even after several weeks of action. The potassium hydrate gave the most positive results. At first there was no apparent change, but after an interval of about ten days or two weeks the plates were found to have completely disappeared, leaving a perfectly clear channel in the cell cavity. A further proof of the resinous character of these plates is to be found in

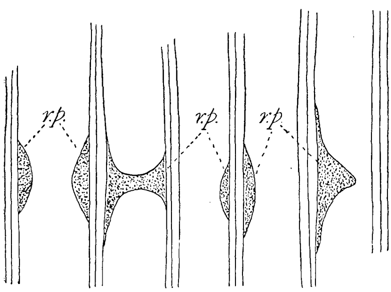

FIG. 34.— *Agathis australis.* Radial section showing the origin of the resin plates (*r. p.*). × 225.

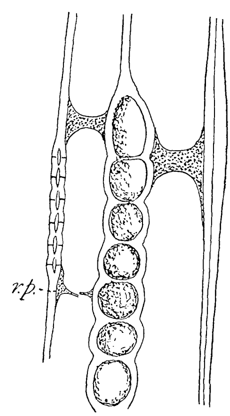

FIG. 35. — *Agathis australis,* Tangential section showing the relation of the resin plates and the medullary ray, and a fractured plate (*r. p.*). × 225.

the ruptures which they not infrequently exhibit (Fig. 35), and in the various developmental stages which may be seen not infrequently (Fig. 34). These show that resin gathers locally upon the inner face of the tracheid wall, and as its volume increases it projects toward the center from all sides, until complete coalescence occurs.

The facts thus obtained proved most conclusively that the transverse plates are obviously resinous and not of the nature of cellulose, even partially, and the conclusion appeared to be justified that they consist of gum dammar, but of a highly modified and highly refractory character. The same evidence also conclusively shows that the cells in which the plates are developed are normal wood tracheids and not wood parenchyma, which is altogether unknown in both Araucaria and Agathis, within the limits of the investigated species.

We are naturally led to ask what is the purpose of these resin plates? The peculiar form in which the resin is deposited, and the particular location of the plates, points with much force to their connection with some functional activity, since if it were simply a question of storage of the secreted products the latter would hardly be disposed as found but rather after the manner common to so many of the Cupressineæ; and this suggestion gains strength from the fact that both in the particular form of the resin masses and their location in the tissue, Araucaria and Agathis are peculiar among all allied genera. No exact comparison can be established with other plants, and it is difficult to suggest an explanation which is adequate. One thing does seem clear, however, and that is that since these plates are of an impervious nature and developed, in some cases at least, in connection with a special constriction of the tracheid cavity, they offer, and possibly they are specially designed to afford, a definite obstruction to circulation in a vertical direction. In this sense they may be designed to serve the same general purpose that is accomplished by the development of thyloses in the vessels of the angiosperms, or in the resin canals of the higher Coniferæ. It is therefore possible that they may be connected in some way not at present clear, with a more complete restriction of the circulation to a radial direction, and

particularly through the medium of the medullary rays as specialized channels for that purpose.

The occurrence of such resinous tracheids is almost exclusively confined to Araucaria and Agathis, in which it is a feature of particular species, but it is a noteworthy fact that similar structures occur, though rarely, among the higher Coniferæ. In the genus Abies they are prominent features in both *A. fraseri* and *A. grandis*. In the former a transverse section shows them to be prominent and scattering through the summer wood, more rarely in the spring wood, while in the radial section the resin is seen to be massive in the summer wood, forming a peripheral layer in the spring wood. In *A. grandis* the resin is usually more abundant, but otherwise the features are the same.

The taxonomic value of the resin tracheids applies exclusively to Agathis and Araucaria, where they are of specific value, and permits of the differentiation of at least one species in each genus. In Abies such tracheids are so sporadic and present so little constancy as to be of no great value.

Returning to a consideration of the resin cells, these structures are found to be entirely wanting in those species of Taxus (4) and Torreya (3) which are included in the present studies. They do occur, however, in Podocarpus where they present the usual structural features, but they are there remarkable for their number and the great abundance of massive resin which they contain. This distribution in the Taxaceæ does not altogether accord with the conclusions of Eichler (11, p. 35) who states that they occur very sparingly in Taxus, but he makes no mention whatever of their presence in Podocarpus where they are much too prominent to escape even the most casual observation.

In the Coniferæ, resin cells are characteristic of all genera except Picea and Pinus, where they are completely replaced by resin passages. They are therefore features in the wood structure of twelve genera, and they are constant characteristics of all their species, with very few exceptions. Such exceptions apply exclusively to the genus Abies, in which four species — *A. fraseri*, *A. lasiocarpa*, *A. veitchi*, and *A. balsamea* — are wholly devoid of such structures.

The recognition of the resin cells presents no difficulty in the great majority of cases because of the abundance and depth of color of the resinous contents. This finds its most complete expression in Taxodium, Sequoia, Cupressus, etc. In Abies, on the other hand, where these cells have experienced extreme numerical reduction and where there also seems to be a corresponding reduction in their secretory power, it is impossible to recognize them in this way. In such cases it is often possible to distinguish them by their slightly different form and somewhat thinner walls as compared with the adjacent wood tracheids; by their situation slightly in advance of the outermost row of summer wood tracheids; and most particularly by their pitted terminal walls when the latter lie near the plane of section. This last feature may also be relied upon in all other cases when any element of doubt is involved (Fig. 36). In longitudinal section the characteristic form of the cell serves to distinguish

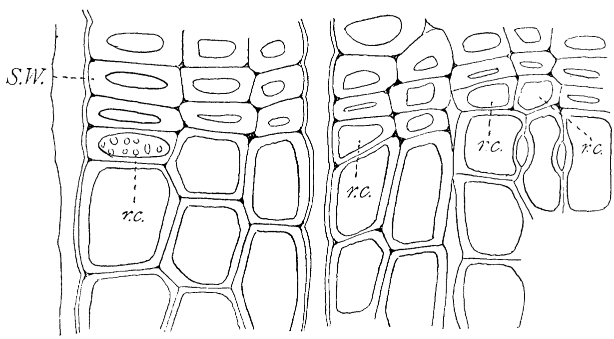

FIG. 36.— *Abies amabilis.* Transverse section showing the positions and structure of the resin cells (*r. c.*) on the outer face of the summer wood (*S. W.*). × 300.

it beyond all doubt, even in the absence of resinous contents. Whether exposed in radial or tangential section, the cell has the form of a narrow cylinder upwards of 300 μ in length, and always several times longer than broad, except in cases where there is a definite tendency, through aggregation, to the formation of resin canals.

The resin cells sometimes occur in pairs, but more generally as isolated structures separated by one or more tracheids. The terminal walls are transverse and more or less strongly marked with simple pits. The side walls, especially the radial, are pro-

vided with simple pits, though often few in number, and this feature serves to a large extent, to assist in their differentiation from adjacent tracheids of similar form (Figs. 36 & 38). It nevertheless not infrequently happens that in transitional forms, such as are met with in *Sequoia sempervirens* (Fig. 37*c*), bordered pits occur on the lateral walls.

The resin is in all cases massive and often very abundant.

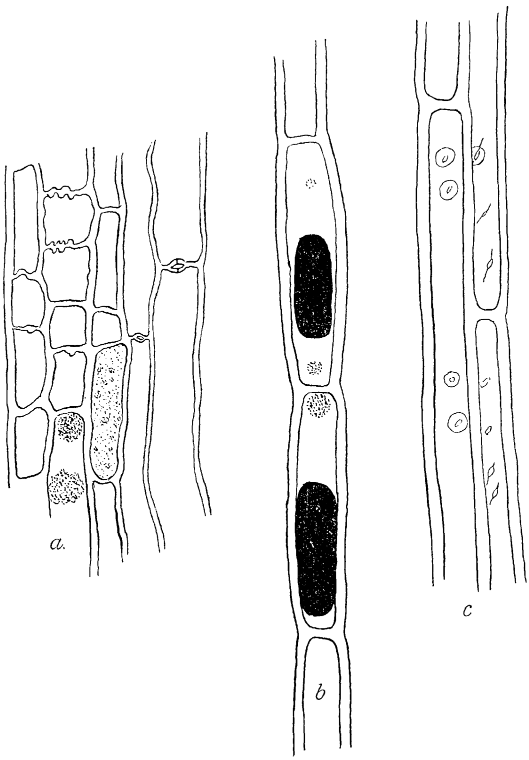

FIG. 37.—*Sequoia sempervirens.* Radial sections showing (*a*) the form of the resin cells and the associated parenchyma tracheids; (*b*) resin cells from the spring wood showing the form of the resin; (*c*) resin cells showing transitional forms with bordered pits. × 200.

In such genera as Taxodium or Sequoia it completely fills the entire cell cavity (Figs. 39 & 40), but in Larix, Tsuga and Pseudotsuga it takes the form of a peripheral layer in immediate contact with the inner face of the cell wall (Fig. 42). The reduction thus indicated is, in some species, carried to such an

extent that the resin is barely recognizable, while in Abies it is wholly wanting.

A relation of more than ordinary interest is to be found in the relation of the resin cells to certain forms of tracheids. In *Sequoia sempervirens* it commonly happens that the resin cells lie in immediate contact with tracheids of special form. These structures are wholly unlike the wood tracheids among which they are found, but they are, in all essential respects, like the tracheids of the medullary rays. They have the form of long, cylindrical elements with abrupt terminations, and they thus bear an external resemblance in form to the wood parenchyma cells with which they are associated. They differ, however, in the distinguishing presence of bordered pits upon their side and terminal walls (Fig. 38*a*). The relations of these two elements is nevertheless a much more intimate one than is implied by mere association. In Sequoia an interchangeable relation is manifested as already pointed out, in the occurrence of resin cells with bordered pits (Fig. 37), while in *Abies amabilis* (Fig. 38) resin cells and tracheids also form a coterminous series. It is thus obvious that we have here precisely the same interchangeable relations that have been found to occur in the medullary rays, and it is evident the one element must arise through modification of the other. The precise order of this sequence is not altogether clear from the available data, but the fact that ray tracheids are derived from their associated parenchyma cells, and that in such types as Podocarpus, Taxodium, etc., the resin cells occur without tracheids, while the latter do occur in Sequoia and especially in Abies, seem to justify the inference that here also they are derived forms, having their origin substantially in special modifications of the parenchyma elements. In view of these relations, it is necessary to distin-

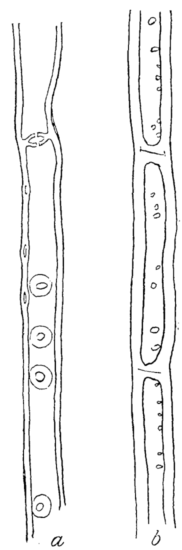

FIG. 38. — *Abies amabilis.* Radial section showing (*a*) the structure of the parenchyma tracheids ; (*b*) the structure of the resin cells : *a* and *b* being normally coterminous. × 200.

guish such elements as *parenchyma tracheids* in order to establish their proper identity and differentiate them from the wood tracheids, which have a wholly different origin, as well as from the ray tracheids, which have a wholly different location. It is probable that the parenchyma tracheids also serve a similar purpose to the ray tracheids with respect to the distribution of nutrient fluids. The origin of the parenchyma tracheids as suggested finds support in the statement of Eichler (11) that the wood parenchyma arises through the activity of the cambium cells, abundantly in the Cupressineæ and Abietineæ, forming in exceptional cases the epithelium of the resin canals, since it at the same time shows how the parenchyma tracheids arise and how they may be intimately connected with the wood-parenchyma; but it finds additional support in a knowledge of the genesis and structure of the resin passage.

In Sequoia and Abies we have two genera which are remarkable for their transitional forms of structure, affording a fairly clear conception of the genesis of the resin passage. In each case there is a well defined tendency toward the aggregation of the resin cells into compact groups which take the form of longitudinal strands, enclosed on all sides by the accompanying parenchyma tracheids. Under such circumstances the individual cells undergo a continual reduction in length until they eventually become but two or three times longer than broad, or they may even become isodiametric. This change is not accompanied by any alteration in the thickness of the walls in the earlier stages of development, but as a result of such a shortening the effect is to bring about the concentration of a greater number of simple pits within a given area. Such cells, therefore, are always more strongly pitted than those which are isolated and of greater length. When aggregates of this sort have attained to a certain degree of development a line of cleavage arises in the center of the mass and results in the formation of an intercellular space which, according to Eichler (11), always arises schizogenously. This space is short and either isodiametric or but little longer than broad, the length coinciding with the principal axis of growth. Such cyst-like reservoirs or sacs represent the primitive form of the resin canal, and they

are typically developed in Sequoia, Abies and Tsuga. They always form a continuous series extending in a direction parallel with the axis of growth; but as the type of reorganization advances they merge, forming a continuous canal such as may be found typically in Pseudotsuga or Pinus. From these statements, then, it is clear that the parenchymatous resin cells undergo modification in two directions, passing into parenchyma tracheids, on the one hand, and on the other becoming shorter

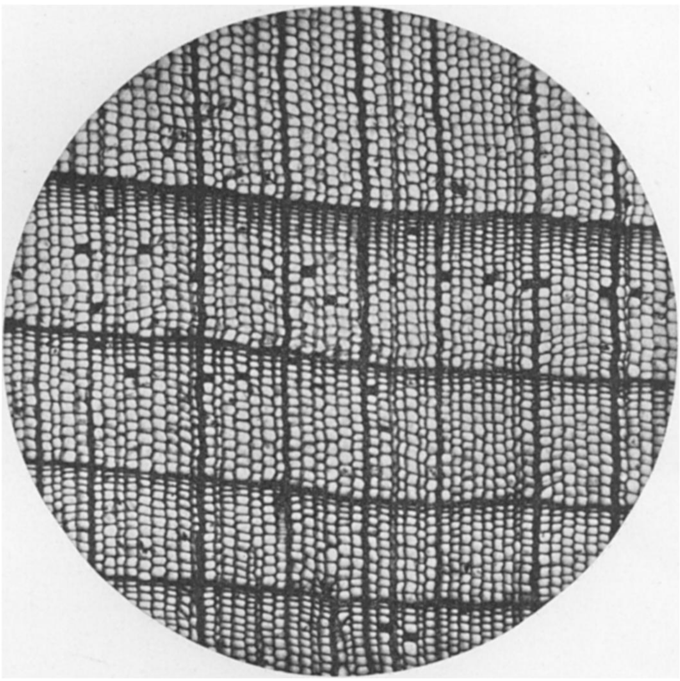

FIG. 39.—*Thuya dolabrata*. Transverse section showing the scattering distribution of the resin cells. × 55.

and shorter, according to conditions of aggregation, until they pass into short cells which eventually constitute the epithelium structure of the somewhat complicated resin passage, the latter thereby becoming the expression of a peculiar aggregation of resin cells. Whatever the stage of development may be, the resin passage is always found to be composed of structural elements arranged in the following order from without toward the center: (1) parenchyma tracheids, (2) resin cells eventually

forming an epithelium and (3) the central reservoir in the form of a cyst or canal. This structure is fully exemplified in the genus Pinus, where the highest form of development is attained.

While the occurrence of resin cells in particular genera is a feature of great taxonomic value, their importance in this respect is greatly emphasized by the particular form of their distribution and the constant tendency they exhibit toward the formation of definite aggregates. In Thujopsis and Cryptomeria (Fig. 39)

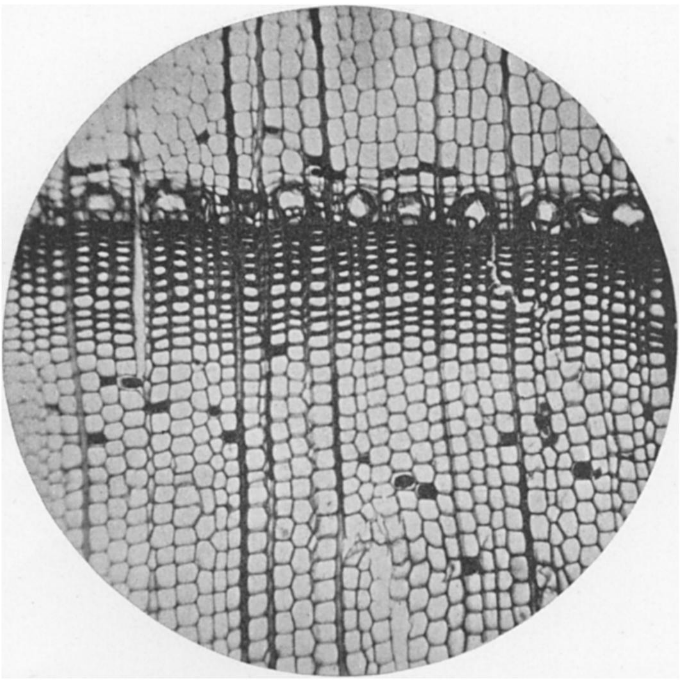

FIG. 40.—*Sequoia sempervirens*. Transverse section showing scattering resin cells in the spring wood, and contiguous resin cysts with aggregates of resin cells on the outer face of a growth ring. × 55.

the resin cells are always scattered throughout the entire transverse section and they show no tendency to the formation of aggregates. In Podocarpus, where there is a notable increase in numbers, the same general law of segregation prevails, but there is nevertheless a somewhat well defined tendency toward aggregation. In Thuya 66.6% of the species show definitely scattering cells, 33.3% show the cells to be scattering with a

tendency toward a more compact disposition, while in 33.3 % the cells fall into well defined aggregates or an approximation to such an arrangement. The genus Sequoia is characterized chiefly by the widely scattering distribution of the resin cells (Fig. 40), but in *S. sempervirens* there are individual cases in which there is also a definite aggregation into groups. In Cupressus 53.9 % of the species are distinguished by the presence of widely scattering cells which become definitely arranged in

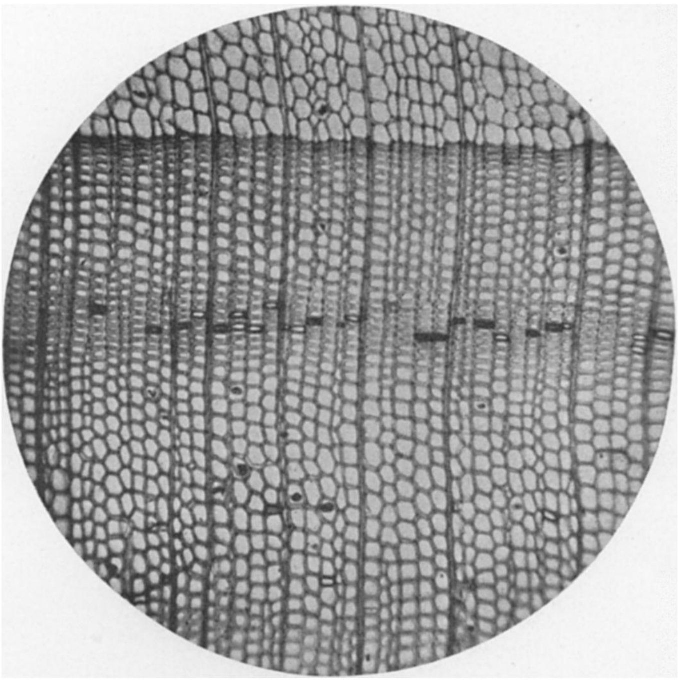

FIG. 41.—*Taxodium distichum*. Transverse section showing the resin cells forming a definite zone. × 55.

zones in 38.4 %, and aggregated into groups in 7.7 % of the species. It will be observed here that this feature of distribution is, on the whole, more pronounced in the relatively primitive genera, and that it diminishes in force in the genera of a relatively high order.

In Taxodium (Fig. 41) and Libocedrus, both of which are distinguished by the presence of very prominent resin cells, these structures are disposed in well defined zones which are concen-

tric with the growth rings and lie either in the spring or summer wood, or in both. This is to be interpreted as a definite tendency to aggregation which is nevertheless not fully expressed, since in each case there are numbers of cells which are not zonal in their distribution, but which conform to the law applicable to Thujopsis and Podocarpus. In Juniperus the cells are typically zonate, being also scattering in only one species. In Abies only 63.6 % of the species bear resin cells. These are

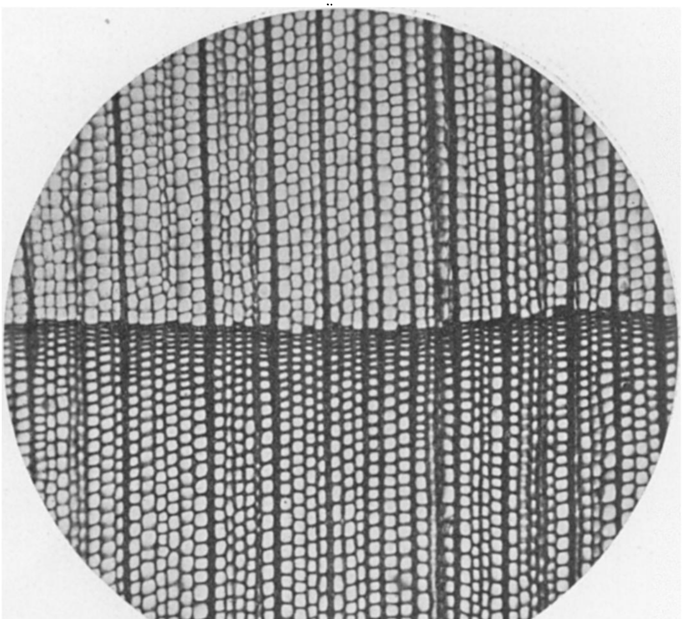

FIG. 42.— *Tsuga pattoniana.* Transverse section showing the distribution of the resin cells on the outer face of the summer wood. × 55.

neither scattering nor zonate in the sense of the previous types, but it is to be observed that in 50 % of such cases, or in 36.3 % of all species, they are aggregated in groups as a preliminary step to the formation of resin passages. On the other hand, 36.3 % of all species show the resin cells to be few, inconspicuous, non-resinous and scattered along the outer face of the summer wood. This, for reasons which will appear more fully later, is to be regarded as a phase in distribution leading to the final

obliteration of such structures, which is fully accomplished in 36.4 % of all the species as represented by *A. balsamea*, *A. fraseri*, *A. lasiocarpa*, *A. veitchi*. This last form of distribution is wholly typical of Tsuga (Fig. 42), in which there are no other resin cells than those on the outer face of the summer wood. Finally, in Picea and Pinus, there are no separate resin cells in any of the situations described, since they have been completely replaced by highly organized resin passages. It thus appears that the distribution of the resin cells presents four variants which bear a direct relation to the organization of resin passages, as the latter eventually replace the former. These facts will appear somewhat more clear from the following summary :

TABLE SHOWING PERCENTAGE DISTRIBUTION OF RESIN CELLS.

	No. of species.	% of occurrence.	Scattering.	In zones.	Grouped.	On the outer face of summer wood.
Ginkgo . . .	1	000.00				
Agathis. . .	1	000.00				
Araucaria . .	3	000.00				
Torreya . .	3	000.00				
Taxus . . .	4	000.00				
Thujopsis . .	1	100.00	100.00			
Cryptomeria. .	1	100.00	100.00			
Podocarpus .	1	100.00	100.00	(100.00)		
Thuya . . .	2		66.60			
	1 = 3	100.00		33.30		
	1		(33.30)			
Sequoia . .	2 = 2	100.00	100.00			
	1				50.00	
Cupressus . .	7		53.90			
	5 = 9	100.00		38.40		
	1				7.70	
Taxodium . .	1	100.00	(100.00)	100.00		
Libocedrus .	1	100.00	(100.00)	100.00		
Juniperus . .	11 = 11	100.00		100.00		
	1		1.10			
Abies . . .	4 = 7	100.00				36.30
	5				45.50	
Tsuga . . .	2 = 5	100.00			33.30	
	5					100.00
Pseudotsuga .	2	100.00				100.00
Larix . . .	4	100.00				100.00
Picea . . .	10	000.00				
Pinus . . .	41	000.00				

Figures in parentheses refer to exceptional forms of occurrence.

From such data it is clear that the distribution of the resin cells bears an important relation to the recognition of sub-generic groups and even of species. But viewing these structures from the broader standpoint of the Coniferales as a whole, it is obvious that they must be placed among the structural elements which belong to the first rank for taxonomic purposes.

We are now in a position to determine what relation, if any, such resin bearing elements bear to questions of phylogeny, and we may first of all consider the resinous tracheids. These structures have been seen to be peculiar to Agathis, Araucaria, and Abies, in which they occur only in certain species. In answering this question, we cannot avail ourselves of evidence derived from fossil plants, since it is in such cases of a negative character. Neither Cordaites nor Araucarioxylon affords definite proof of the presence or absence of such structures, since they do not appear in any of the published diagnoses, and our own studies have not resulted in their recognition. If originally present, they must have been obliterated in the course of fossilization. We must therefore depend entirely upon such evidence as is afforded by existing species. From this point of view it is obvious that they furnish no evidence as to the origin of either of the three genera in which they occur. It is, on the other hand, possible to determine from other data, that both Agathis and Araucaria are much inferior to Abies in point of structural organization and development, and from this we may be permitted to conclude that the resin tracheids of Abies are vestigial forms of elements which were typically developed in Agathis and Araucaria, and possibly characteristic also, of their progenitors. If such inferences are to be regarded as justifiable, they go far to support the idea of a common origin for all three genera, and they thus lend force to conclusions which lead to the same result, but upon the basis of independent data.

From a study of the distribution of the resin cells, it is apparent that they fall into four categories in which the typically segregated cells may be held to represent the most primitive form of disposition. This view is greatly strengthened by the observation that in all such cases, the resin cells are rarely if at all accompanied by parenchyma tracheids, while the structure of

the cell is farthest removed from that which is found to enter into the composition of resin passages, whence they are also to be regarded as of a primitive character. This view is supported by the observed fact that those genera and species in which such segregations occur, are also of a relatively primitive type. With an advance in organization, there is a tendency to the formation of aggregates as expressed in the zonal distribution of Taxodium, Libocedrus or Sequoia, where we also find the definite formation of groups of cells which later exhibit the initial stages in the formation of a definite canal. But in Sequoia, as also in Abies where similar changes take place, the more complete aggregation of the cells is invariably accompanied by structural alterations whereby they become greatly shortened and more strongly pitted, while they are always accompanied by parenchyma tracheids with which they are interchangeable. In this connection it is also to be noted that the aggregates in Sequoia, Abies and Larix leading to the formation of resin sacs, are always disposed in a zonal manner, conformably to the zonal disposition of the separate elements, a relation which is in direct harmony with the view already advanced, that the zonal disposition of the isolated cells is an advance upon the strictly segregated form, and that it leads directly to the formation of resin passages. Following upon the zonal distribution, a more complete aggregation results in the formation of local groups of short, resin cells ultimately leading to the formation of a true resin canal. Such a feature of distribution, occurring in genera which, from other data, may be shown to be relatively high in development, is in itself significant ; but we further find that the scattering, zonal and grouped forms bear such relations to one another, that the real succession is in the order already given. Thus while both species of Sequoia are characterized by scattering cells, *S. sempervirens* also shows them aggregated to form groups and eventually imperfectly organized resin canals. Or in Cupressus, the transition is expressed in a more complete form, involving all three modes of distribution. In Tsuga there is an obvious tendency toward the elimination of the resin cells which are now greatly reduced in numbers and confined to the outer face of the summer wood. In Abies a similar tendency is also manifested,

but it is expressed in a different way, and just here we must note a fact of more than ordinary significance. Resin cells are present on the outer face of the summer wood in *A. grandis*, *A. concolor*, *A. amabilis* and *A. magnifica*. Groups of resin cells are present in *A. nobilis*, *A. concolor*, *A. bracteata* and *A. firma*, but it will be seen that in only one case — *A. concolor* — are the two forms of distribution presented in the same species. This is in direct conformity with the idea that the resin passage eventually displaces the resin cell, bringing about an obliteration of the latter, and it goes far to support the idea that with respect to these particular structures, the genus Abies occupies a transitional position, standing next to Picea and Pinus, from both of which the resin cells have completely disappeared. Furthermore, from another point of view, the gradual replacement of the resin cells appears to be indicated by a corresponding reduction in the contained resin. Nowhere is the resin so abundant in the resin cells, as in those genera like Podocarpus and Taxodium, which show no development of resin passages, even in their most simple forms; but with the development of resin sacs, as in Abies or Sequoia, or of resin passages as in Larix and Pseudotsuga, there is a remarkable diminution of the resin, apparently in direct response to its more ready production by more specialized structures.

The genus Abies then, appears to form a transition group, having parallelisms with Agathis and Araucaria through the occurrence of resinous tracheids; with Thuya, Cupressus, etc., through the survival of isolated resin cells approaching obliteration; with Tsuga, Larix and Pseudotsuga through the development of rudimentary resin canals leading to the formation of definite resin passages; and with Sequoia through the survival of isolated resin cells and the development of rudimentary resin canals. Through these parallelisms the connection appears to be most direct on the one hand with Sequoia, and on the other with Tsuga. This relation of Sequoia to Abies has been shown by Penhallow on former occasions (38), and has more recently been indicated in other ways by Jeffreys (24), but so far as the present evidence is of value, it would not permit us to infer that Sequoia, Abies and Tsuga form a continuous and coterminous

series in the order given, but rather that they represent separate, though short, side lines of development, between which the general sequence is manifested.

Resin Passages.

Structural.

Our studies of the resin cell have shown how peculiar aggregates of these structures lead in a natural way to the organization of resin passages, the structure of which it is now necessary to discuss somewhat in detail, and in doing so it will be most profitable to have reference to (1) the primitive form, (2) the intermediate form and (3) to the advanced or fully organized form.

The primitive form of the resin passage is to be found in Sequoia, Tsuga, and Abies and inasmuch as within these genera they exhibit differences in organization which correspond approximately to the sequence given, it will be necessary to discuss them somewhat in detail, with special reference, however, to Sequoia. This genus possesses special interest with respect to the occurrence and organization of secretory reservoirs, since it is in all probability not only the most ancient genus in which such structures occur, but it is, so far as I am aware, the only genus affording special data with respect to important variations of structure and mode of occurrence. Being also, on the whole, the most primitive of the three genera, I shall deal with it first.

In *Sequoia sempervirens* the secretory reservoirs occur in rows within the initial layers of the spring wood, and they therefore lie exactly on the outer face of the summer wood of the previous year. Within this row the reservoirs are contiguous and in many cases they become confluent so as to form a more or less extended and continuous compound reservoir lying tangentially. In their most rudimentary forms they present the aspect of simple aggregates of resin cells without any differentiation of a resin sac or of an epithelium. In a more advanced stage of development there is produced a central cavity in the form of an intercellular space (Fig. 43, *C*) which has obviously

originated schizogenously. About this the resin cells are generally flattened radially and disposed in such a manner as to suggest the future development of a definite, limiting layer or epithelium. In the completed form of the structure the central space has broadened out and taken a circular form, assuming the character of a definite cyst bounded by as definite a limiting epithelium in which the cells are always flattened radially and disposed concentrically (Fig. 43, *C*). Externally to these cells there may be a second layer of similar resin cells, constituting the outer epithelium, while the whole is enclosed on three sides by a layer of parenchyma tracheids which are exceedingly like

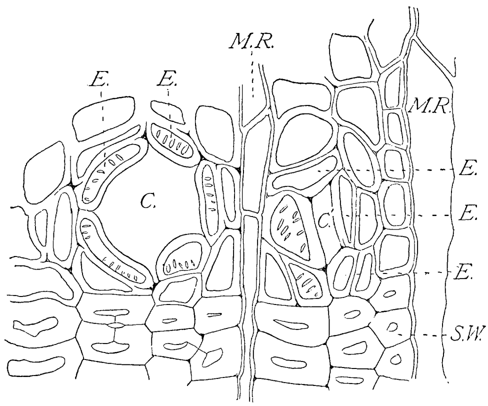

FIG. 43.—*Sequoia sempervirens.* Transverse section showing two contiguous resin cysts, *C*, completed and with a normal epithelium *E*; *C'* an intercellular space as the rudiment of a cyst with imperfectly developed epithelium.' *M. R.* the medullary ray; *S. W.* the summer wood. × 225.

the associated tracheids of the spring wood, but from which they may usually be distinguished by (1) their greater size and relatively thinner walls, (2) the occurrence of bordered pits on the tangential and terminal, as also upon the radial walls. Such parenchyma tracheids never occur in the adjacent summer wood for very obvious reasons, but on the radially opposite side of the reservoir they are very commonly flattened radially (Fig. 43), and they not infrequently present the same structural aspects as the epithelial cells. The interchangeable relation between resin cell and parenchyma tracheids as already shown would lead us to suspect a substitution in the composition of the epithelium, and

such substitution does actually occur, since it is often to be noted that the second and third rows may be made up, at least in part, of tracheids.

In a longitudinal radial section the reservoir is found to have the form of a sac of varying form and size, but generally elongated parallel with the axis of growth and completely closed at both ends (Fig. 44). The epithelium which immediately defines the limits of the sac generally consists of short, cylindrical cells, while in the second or outer layer the cells become much elongated and several times longer than broad. Beyond this, the third layer consists of parenchyma tracheids readily distinguishable whenever the terminal walls lie near the plane of section, or otherwise as already indicated. Certain deviations from this typical structure require examination. The resin sacs are placed in vertical series of indeterminate extent, but at varying intervals of such a nature that they may sometimes be separated only by a rather thick wall of short resin cells. At other times they are somewhat distant and separated by an extensive vertical tract of resin cells. From this it is obvious that in any given plane of section there will be a great diversity of aspects presented, but in the main exhibiting structural gradations in the development of the reservoir as already recounted. In some cases thick-walled cells of circular outline may be seen

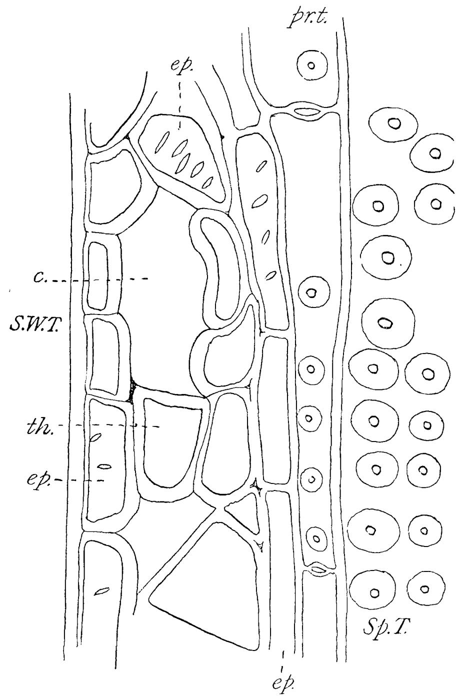

FIG. 44.— *Sequoia sempervirens.* Radial section of a resin cyst, showing the epithelium (*ep.*); the central cyst (*C*) with a thylosis (*th*); parenchyma tracheids (*pr. t.*), and a tracheid of the spring wood (*Sp. T.*). × 300.

in transverse section to stand out from the general line of the epithelium and lie within the cavity proper. More rarely such cells are so multiplied as to fill the entire cavity, and they may themselves be filled with granular resin. Such features are

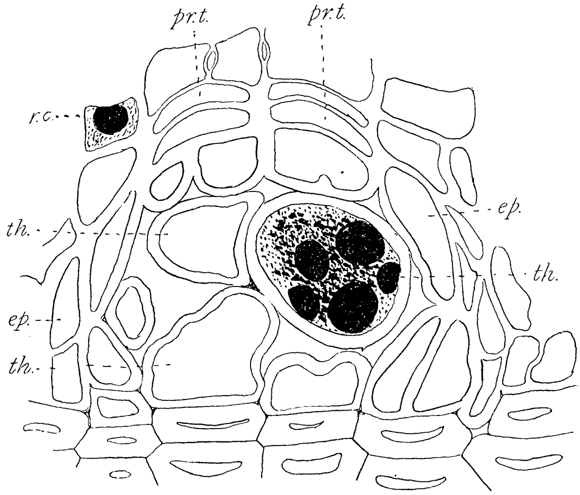

FIG. 45.—*Sequoia sempervirens.* Transverse section of a resin cyst showing an associated resin cell (*r. c.*); the epithelium (*ep.*); the thyloses (*th.*), one of which contains resin, and one of which is directly derived from an epithelium cell; the parenchyma tracheids (*pr. t.*). × 300.

clearly defined (Fig. 45), and it is evident from the way in which such cells originate from the epithelial cells that they are of the nature of thyloses. A longitudinal section through such a reservoir (Fig. 46) shows how such thyloses occupy the entire cavity of the cyst, while in other cases they may be purely local (Fig. 44). Among fossil sequoias similar thyloses form a most characteristic feature in the resin passages of the medullary rays in *S. burgessii.*

In *Tsuga caroliniana* there are no secretory reservoirs, but just in the region between the spring and summer wood of the same growth ring there are peculiar aggregates of resin cells of a more or less rounded outline but forming a continuous series of considerable extent. An analysis of these aggregates shows them to be composed of thick-walled and rounded resin cells, among which there may be a small central intercellular space without any definite organization of epithelium. In such aggre-

gates the component cells are far less resinous than the isolated resin cells of the same section. The parenchyma tracheids are not clearly distinguishable from the associated wood tracheids. In radial section the cells are seen to be very variable, thick-walled and sometimes with more or less prominent intercellular spaces. Between the rays they are several times longer than broad, but opposite the rays they are short, cylindrical and more copiously pitted: while sometimes they may be seen to merge into ray elements and thus to continue their course at right angles to their primary direction. A careful comparison of these cell aggregates with those of Sequoia and Abies leaves little room for doubt as to their structural and functional identity, and we cannot do otherwise than conclude that they represent the most primitive structural condition which is capable of directly giving rise to definite cysts by central cleavage.

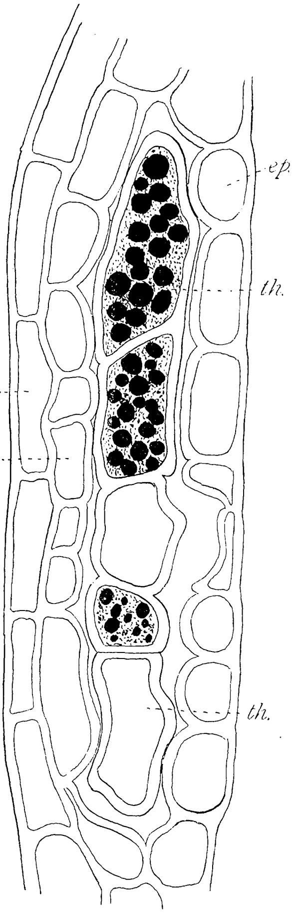

FIG. 46.— *Sequoia sempervirens.* Radial section of a resin cyst showing the epithelium (*ep.*), and the thyloses (*th.*) which completely fill the cyst, and several of which are resinous. This figure corresponds to Fig. 45. × 225.

In *Tsuga mertensisana* the secretory reservoirs are disposed like those of Sequoia, on the outer face of the summer wood, where they form tangential series. They exhibit all the gradations from simple cell aggregates without a central space to perfectly formed cysts with a definite epithelium. This latter is in one, more rarely in two rows, and it is composed of more or less rounded or radially flattened elements. The parenchyma tracheids are few in number, and they are not readily distinguishable from the adjacent wood tracheids. In

longitudinal section the reservoirs are variously rounded or oblong cysts, contiguous or isolated, and forming a longitudinal series. In their general form and structure they are essentially the same as in Sequoia.

In the genus Abies secretory reservoirs occur in at least four species where they form more or less extensive tangential series, within which they are usually contiguous and more or less confluent. They present the same general variations in structural organization as in Tsuga and Sequoia, but in *A. concolor*, and less conspicuously in *A. nobilis*, they are often extended in a radial direction so as to become narrowly oval or oblong, and several times longer than broad. The epithelium consists of a well defined structure composed of one to three rows of cells. The first row, immediately bordering upon the canal, consists of rounded or oval and thick-walled cells which are much smaller than those of Sequoia, and similar to those of Tsuga. They are always characterized by an abundance of strongly defined, simple pits, and many of them contain resin, which usually takes the form of rounded granules of diverse sizes. The parenchyma tracheids are so nearly like the accompanying wood tracheids as, in some cases, to be separable with some difficulty, but they generally surround the resin sac, at least within the limits of the spring wood, and they not infrequently replace the parenchyma cells of the epithelium more or less completely. Not infrequently they form somewhat extended radial series from the epithelium into the spring wood, as in Picea (Fig. 48). In such cases they are usually recognizable by their rather unusual size and thinner walls, and in addition they commonly show bordered pits on the tangential walls. When the terminal wall lies sufficiently near to the plane of section, it shows from one to several rather large bordered pits, and by this feature such tracheids may be located with much certainty. Thyloses have been definitely noted only in the case of *A. concolor*, in which species they are essentially of the same general character as in Sequoia, They are thick-walled and either isolated or so numerous as to fill the entire cyst. In one case of contiguous cysts, an epithelial cell was found to form thyloses in both cysts — in the one case giving rise to an isolated cell, in the other forming a tissue which nearly filled the entire cavity.

In radial section the reservoirs are round or oblong cysts of variable size, and they are either contiguous or distant. In the former case they rarely or never become confluent, but they maintain their separate identity as in Sequoia and Tsuga. In the latter case the intervening region is occupied by an aggregate of resin cells in all essential respects like those in the same regions of Sequoia and *Tsuga mertensiana*, or like the aggregates which are generally characteristic of *Tsuga caroliniana*. The inner epithelium usually consists of short, cylindrical and strongly pitted cells which, in the second and third rows, become successively longer and less strongly pitted, so that those in the outer row may be identical in form and markings with the isolated resin cells. In the two outer rows the cells not infrequently show bordered pits on their radial walls, thus presenting transitional forms which gradually pass over into tracheids, and the one then replaces the other. The parenchyma tracheids, which are always most characteristic of the spring wood, are always distinguished by the presence of large and prominent bordered pits, but in addition they are sometimes broad and thin-walled, and lie in radial series.

From these facts it is clear that the secretory reservoirs of the three genera in question always take the form of closed sacs, which DeBary has already pointed out as a feature of certain Coniferæ (9, p. 440), and in order to clearly differentiate them from those which occur in the higher Coniferæ, I shall reserve for all such cases the term *resin cyst*. That such sac-like reservoirs represent the primitive form of the resin passage scarcely admits of question when we observe the various transitional forms which they present and the relation they bear to the resin passages of the higher Coniferæ — a view which is strengthened by the observation of DeBary (9, p. 443) that primitive forms of the secretory reservoir occur in the pith of Ginkgo in the form of elongated sacs.

DeBary has shown (9, p. 440) that the secretory passages traverse the wood longitudinally, at first as prismatic tubes which usually acquire a round or elliptical, transverse section. This statement is applicable to Pseudotsuga, Larix, Picea and Pinus, but inasmuch as there are important differences of detail between

the first three genera and the last, in such a way that the former represent an intermediate, while the latter represents a completed type, it will be necessary to examine them separately. In all of these cases, however, the secretory reservoir is invariably characterized by the presence of a definite and continuous canal of indeterminate length, in consequence of which I reserve for them the appropriate and long used term, "resin passage," as distinguished from the resin cysts of the previously discussed genera.

In Pseudotsuga the resin passages are always scattering, though they frequently occur in tangentially extended groups of two or four contiguous or even coalescent reservoirs. The central canal, which is usually small and not infrequently very narrow, is rather more generally rounded than in previous types. The epithelium is very clearly defined and consists of one to three rows of thick-walled parenchyma cells, sometimes containing resin, the first row of which are rather small and radially flattened, but in *P. macrocarpa* they are rather thin-walled. In *P. douglasii* the epithelium is commonly extended on the two sides of the resin canal in such a way as to form a tangentially elongated tract which not infrequently extends beyond and involves neighboring medullary rays. In *P. macrocarpa*, on the other hand, the epithelium is concentric with the canal, thus forming a tract of about equal thickness all around. Such a deviation as is expressed in *P. douglasii* constitutes the first evidence of a tendency in development which is fully and frequently expressed in Pinus. Thyloses are of infrequent occurrence, and they appear to be confined to *P. macrocarpa*, where they are few in number and generally rather thin-walled. Parenchyma tracheids are usually not apparent in a transverse section. This results from the frequent location of the resin passages in the summer wood, which is not favorable to their development, and from the close resemblance which they bear to the tracheids of the spring wood; and while such elements form an integral part of the resin passage, their particular disposition cannot be exactly defined, though there is no good reason for supposing that they differ in this respect from what may be observed in other cases. In a longitudinal section the

canal is found to be more or less continuous, though it presents frequent constrictions, and it is thereby reduced to very narrow dimensions. It is this feature which causes the canal to exhibit such marked variations in size when seen in transverse section. The epithelium cells are narrowly cylindrical and rather long and thick-walled, as well as somewhat strongly pitted. Outwardly they become much longer and relatively narrower, and they eventually merge with the surrounding parenchyma tracheids by which they may also be replaced.

In Larix the same features of contiguity and coalescence may be observed, except that in *L. occidentalis* the resin passages sometimes form into continuous zones of imperfectly organized structures with the aspect presented in *Tsuga martensiana.* The epithelium is always well defined (Fig. 47) and it consists of one, sometimes two, rows of cells. The cells of the first row are small, very variable in form and size, thick-walled and more or less strongly flattened radially. They are also commonly resinous and more or less strongly pitted. When there is a second row of epithelium, the cells are essentially like the wood tracheids, and like the parenchyma tracheids from which they may be separated with difficulty. The latter, therefore, which are absent from the summer wood, can be distinguished from the elements of the spring wood only when the pits on the terminal walls (Fig. 47 *pr. t.*) are brought into view, or, more rarely, when the pits on the tangential walls are in evidence. Thyloses rarely occur, and so far they have been noted only in *L. occidentalis*, where they

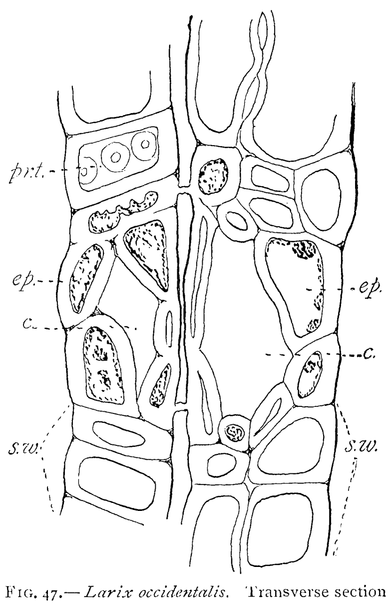

FIG. 47.—*Larix occidentalis.* Transverse section from the inner spring wood showing a pair of resin passages with the central canals (*c*); the thick-walled epithelium (*ep*); a parenchyma tracheid at (*pr. t.*) and the summer wood (*s. w.*). × 300.

are infrequent and thick-walled, and in *L. americana*, where they are of rare occurrence and thin-walled. In longitudinal section the central canal is always continuous, though constricted at intervals, a feature in all essential respects the same as in Pseudotsuga. Radially, the first row of epithelial cells are short cylindrical, or in *L. occidentalis* short fusiform, but there is a graduated increase in length outwardly, so that in the second, or in the third row if present, they become narrow and very long, and they eventually merge with the parenchyma tracheids through intermediate forms with bordered pits. All of the epithelial cells are thick-walled and strongly pitted, and they thus offer a somewhat strong contrast to the rather thin-walled parenchyma tracheids with bordered pits.

The resin passages of Picea differ from those of Pseudotsuga and Larix in being more strictly segregated, and in consequence there is a conspicuous absence of contiguous structures, which may nevertheless sometimes be seen in *P. nigra*, and especially of coalescent forms. They are usually narrow, but well rounded or oval, and there is far greater uniformity of structure and form than in any of the preceding types. The epithelium consists of one row, one to two rows, or even one to three rows of cells, differences which apparently belong to particular species, though no attempt has been made to define the precise limitations of such features. The cells are generally small, round or radially flattened and thick-walled, though occasionally a cell may be thin-walled as in *P. alba*. In cases of thick-walled epithelium, the outermost cells merge with similar tracheids from which they are not readily distinguishable, while the general epithelium becomes extended into a tangentially elongated tract as in *Pseudotsuga douglasii* and Pinus. Thyloses have been noted as of occasional occurrence in *P. nigra*, *P. pungens* and *P. sitchensis*, but they are always thin-walled. Parenchyma trachieds are not obvious in the summer wood, but they are recognizable in the spring wood where they appear to replace the resin cells, though they are apparently of much less frequent occurrence than in the genera previously discussed. In *P. alba*, however (Fig. 48, *pr. t.*), we sometimes find a radial series of tracheids which also extends laterally so as to form an enclosing

layer. Radially the canal is continuous, but with more or less frequent constrictions as in Pseudotsuga and Larix. The epithelium consists of narrow, cylindrical and much pitted cells which increase in length in the outer layers where they become five to seven times longer than broad, and finally they merge with the parenchyma tracheids which replace them.

While the general composition of the resin passage in Pseudotsuga, Larix and Picea is the same as that of the resin cyst, it is obvious that the frequent constrictions in the canal indicate a partial survival of the cystic formation. We must therefore regard these structures and the three genera to which they belong as forming a transition group between the primitive resin cyst on the one hand and the perfectly organized resin passage of Pinus, with its canal of uniform width, on the other.

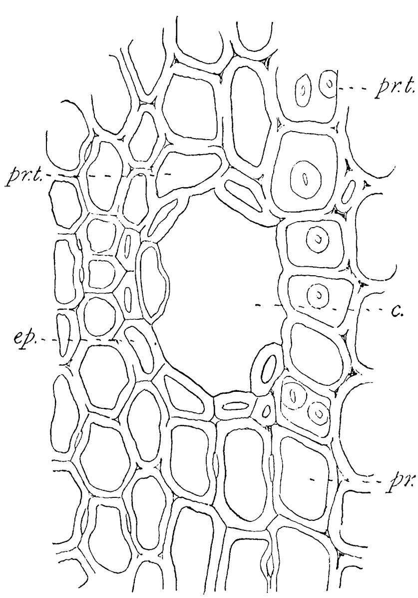

FIG. 48.—*Picea alba.* Transverse section of a resin passage from the spring wood, showing the central canal (*c*); the thick-walled epithelium (*ep.*) and the parenchyma tracheids (*pr. t.*). × 300.

In the genus Pinus, the resin passages show considerable variation in detail, but they all conform to the same structural type (Fig. 49). The central canal is broad and round, often very large, and in longitudinal section it is a perfectly continuous passage of uniform width. The epithelium consists of large, but very variable and thin-walled cells in one to several rows. In the soft pines it generally forms a concentric zone of uniform width, but in several of the hard pines there is a marked tendency to extension in a tangential direction and the formation of rather extensive eccentric tracts. In all of the pines there is a pronounced tendency for the epithelial elements to become so thin-walled that they are readily broken out in

making sections, while in the hard pines, as *P. cubensis*, *P. tæda*, *P. pungens*, etc., the cells are often strongly resinous. In the outer epithelium, the thin-walled elements may be associated with occasional thick-walled elements with which they are interchangeable, precisely as in the similar relations displayed by the medullary rays of *P. pungens* and *P. cubensis*. In the same region also there is a similar association with and transformation

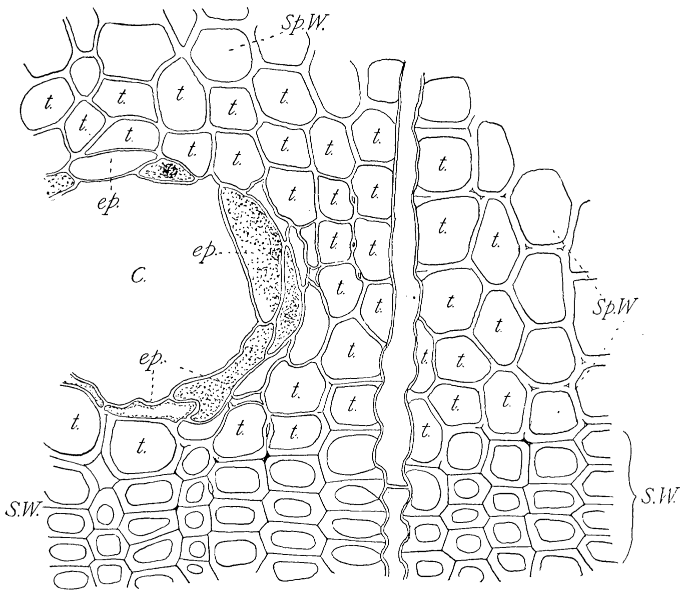

FIG. 49.—*Pinus reflexa*. Transverse section of a resin passage from the inner face of the sping wood showing the central canal (*C*); the thin-walled and resinous epithelium (*ep*); the parenchyma tracheids (*t*); the spring wood (*Sp. W.*) and the summer wood (*S. W.*). × 225.

into parenchyma tracheids, which also has its parallel in the medullary ray. Somewhat more specifically, special reference to two examples may serve to illustrate the general nature of some of the more important variations. In longitudinal section the parenchyma tracheids are usually of much greater length than the associated parenchyma cells, with which they are parallel or coterminous, and they occur in large numbers in *P. lambertiana*. In *P. reflexa* they are coterminous with parenchyma cells which they finally succeed, to be replaced in turn by thin-walled wood tracheids. In *P. lambertiana* they are

always to be distinguished by the bordered pits on the radial, tangential and terminal walls, while in *P. reflexa* they are characterized by the large number of bordered pits on the radial walls, with very few on the tangential walls. In the former situation the pits are much smaller than in adjacent wood tracheids. Together with adjacent wood tracheids, the parenchyma tracheids may be more or less involved in bearing resin (*P. lambertiana*), while finally, as exhibited in transverse section, their numbers may be so large that they form extensive areas about the resin passage (Fig. 49). In such a case the sequence of elements in transverse section would be :—

1. Canal with thyloses.
2. Thin-walled epithelium.
3. Epithelium — cylindrical parenchyma tracheids.
4. Parenchyma tracheids.
5. Wood tracheids with thin walls.

Thyloses are a constant feature in the structure of the resin passages of Pinus (Fig. 30). They are always thin-walled and completely fill the canal. So constant are these features in association with those previously recounted that they serve to afford a ready means of accurately recognizing the genus under all circumstances.

The general course of development thus outlined shows that the parenchyma tracheid stands in such relation to the organization of the resin passage that its more frequent occurrence is directly correlated with a higher type of organization and development in the plants to which they belong.

We are now in a position to present a general summary of the relations which the resin cells bear to the organization of the secretory reservoirs — cysts and passages — and the position which the latter occupy in the economy of the plant, as follows :

1. Resin cells, which are of the nature of wood parenchyma, at first occur as isolated structures filled with resin, but they show a definite tendency to association, and later form definite aggregates.
2. Parenchyma tracheids become associated with such aggregates for the purpose of effecting a more complete nutrition of the secretory cells.

3. Resin cells, when aggregated beyond a certain point, develop schizogenous, intercellular spaces which form either central, closed cysts, or central canals of indeterminate length.
4. The structure of the cyst or passage always presents the same sequence of elements, and the work of the reservoir is then divided between
   (a) the tracheids which provide nutrition for the secretory cells;
   (b) the secretory cells or epithelium in which the formation of the resin takes place;
   (c) the cyst or canal which provides an outlet or storage reservoir for the surplus product;
   (d) the thyloses which may impede the proper storage of the resin, or which may individually serve the purpose of storage.

So long as the formation of resin is not excessive, it is stored in the cells where produced. This is true of all isolated resin cells, as well as of many which enter into the composition of complex cysts and passages. When the resin is excessive, however, the surplus is excreted into specialized reservoirs of the form of closed cysts, or of canals, and we are led to interpret the appearance of these structures in the higher Coniferæ as a response to such needs. The development of the resin passages will thus be seen to stand in direct relation to the capacity of the plant as a resin producer — a fact which is otherwise apparent from our knowledge of the general capacity of the different genera as resin producers, and a comparison of this feature with their known position in the line of descent.

(*To be concluded.*)